Breeding Better Livestock

by RALPH W. PHILLIPS

THE BREEDER uses three basic tools to bring about the genetic improvement of animals. They are selection, inbreeding, and crossing. The tools have been used to develop existing breeds; they will be used to effect further improvement in breeds, establish new types and breeds, and raise the productivity of commercial livestock. Besides them, the breeder uses a knowledge of the physiology of reproduction to insure maximum fertility and maximum opportunity for selection.

The breeder's ability to select superior animals as parents of the next generation is one of the most important of the factors that determine progress in animal breeding. If the breeder is to select genetically superior animals, he must have yardsticks that measure that superiority. And if he is to utilize effectively in selection the knowledge he obtains through application of those yardsticks, he must know which selection procedures will result in greatest progress. Several recent studies have yielded important information on those points.

A breeder may use one of the three basic methods of selection. These are: First, the "tandem" method, in which he selects for one character at a time until it is improved, then selects for another one, and so on, until all desired traits are improved; second, the "total score" method, in which selection for all desired traits is practiced simultaneously, the total score or index being constructed by adding into one figure the credits and penalties given each animal according to its superiority or inferiority for each trait considered; third, the "independent culling levels" method, in which he sets a certain level of merit for each trait, and discards all individuals below that level, regardless of their rating in other traits.

A careful investigation of the efficiency of the three methods of selec-

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tion was made by L. N. Hazel and Jay L. Lush, of Iowa State College. From their study of the theories involved, they conclude that selection for a total score or index of net desirability is more efficient than selection on the basis of independent culling levels, and that the tandem method is the least efficient of the three methods.

Although selection on the basis of independent culling levels is generally less efficient than selection for total score, it does permit earlier selection for some traits, without waiting for other traits for which selection can best be made at later ages. The superiority of the independent culling level over the tandem method increases with the number of traits involved and the intensity of culling.

Dr. Hazel also studied the principles of constructing and using selection indexes, or the "total score" method of selection. He points out that the genetic gain that can be made within a group of animals by selecting for several traits at once is the product of the selection differential, or intensity of selection—the superiority of selected animals over the average of the entire group—the multiple correlation (a measure of relationship) between aggregate breeding value and the selection index, and genetic variability. The first of these, the selection differential, is limited by the rate of reproduction of each species, and it may be small because of the breeder's carelessness in making selections or in emphasizing unimportant points. The third, genetic variability, is relatively beyond man's control. Hence, the greatest opportunity for increasing progress from selection is by insuring that the second, the multiple correlation, is as large as possible.

Hazel gives a multiple correlation method of constructing indexes having maximum accuracy. To use it, one must know the constants:

- 1. Relative economic values for the different traits.
- 2. Standard deviations (measures of variation) for each trait.
- 3. Correlations (measures of relationship) between each pair of traits.
- 4. Heritability of each trait (a measure of the extent to which expression of trait is governed by heredity).
- 5. Genetic correlations between each pair of traits.

The genetic correlations show the extent to which traits are similar because of genes that affect both traits, and are determined by correlating one trait in one animal with the other in a relative. Using these principles, Hazel developed three indexes for swine. The first involved two characters for which data were available before breeding age. The index (I) was:

$$I = (0.137 \times W) - (0.268 \times S)$$

in which W is the pig's weight at 180 days and S is the pig's market score. The second index was:

$$I = (0.136 \times W) - (0.232 \times S) + (0.164 \times P)$$

in which W and S are the same as in the first formula and P is the productivity of the dam, used as a measure of the pig's productivity, the lapse

of one generation being compensated for by a suitable adjustment for the heritability of this trait.

The third index was designed to include information about the average weight (W) and score (S) of the litter in which each pig was born, in addition to the three traits in the second index. These were considered as fourth and fifth variables, using the correlations between the various traits and making allowances for the number of pigs per litter when arriving at the values to insert in the index.

The three indexes were compared to determine their relative efficiency in making genetic progress. This rate of progress is proportionate to the size of the correlation between genotypes of the selected animals and their indexes. The second and third indexes were 8.8 and 11.3 percent, respectively, more efficient than the first. Since the time and effort expended in keeping records is but a small fraction of the total labor connected with a breeding program, the second index would probably be preferable to the first in most cases. The third might also be chosen over the second, since genetic progress could be increased a little more through its use, and the extra labor would be only that of computing and using the litter averages from data already available.

The progress that could be made by using the three indexes studied by Hazel was 36.3, 39.5, and 40.4 percent, respectively, of that which could have been made by a perfect index, or one in which the phenotype, or appearance of the animal, was a perfect measure of the genotype, or genetic make-up, of the animal. The loss is due to the confusing effects of environment, dominance of one gene over its pair-mate, so that the recessive member of the pair is not evident in the phenotype, and epistasis, or interaction of genes, all of which can make phenotypes unlike genotypes.

A selection index for Rambouillet sheep has been developed at the Western Sheep Breeding Laboratory at Dubois, Idaho, based on the same principles as those outlined for swine indexes. These traits have been included: Face covering (F), length of staple (L), weaning weight (W), type score (T), condition score (C), and neck-fold score (N). The completed index (I) is as follows:

$$I = 75 - (15 \times F) + (7 \times L) + W + (0.4 \times T) + (7 \times C) - (11 \times N)$$

The constant of 75 is added to insure that the index will be positive and average around 100. Corrections for various factors, like twinning, age of dam, and inbreeding, may be made directly on the index, using suitable correction constants. The completed index varies from about 70 to 150 for individual lambs in the Rambouillet flock at Dubois, with an average of about 110. The value of the index may be estimated by comparing the progress when the index was used with that before it was available. Progress was roughly determined by combining the selection differentials for the various traits after each was weighted by

its heritability and its economic importance. Over-all progress from selection at weaning age was increased in the range of 20 to 50 percent by the use of the index.

The breeding merit of an animal may be estimated in various ways, including the merits of its ancestors, the animal's own characteristics and performance, the merit of collateral relatives, such as sibs (brothers and/or sisters) and half sibs, and the merit of its offspring.

The last is usually called the progeny test. Much has been written concerning its accuracy, compared to that of other methods that might give indirect measures of breeding merit. From the standpoint of rate of genetic progress, factors other than relative accuracy must be considered. The most important of these factors are the age at which progeny tests may be obtained and the rate of reproduction. The longer interval between generations that results from use of the progeny test tends to offset the advantage gained by more accurate selection, and may actually reduce the annual rate of improvement.

The relative merits of progeny testing and other methods of selection have been studied by G. E. Dickerson and Dr. Hazel. This is an intricate problem requiring detailed mathematical studies in order to obtain a solution. They considered a number of traits in various species, and concluded that the possibilities of increasing progress by a regular plan for use of progeny-tested sires are limited to certain kinds of livestock and to certain traits. The reasons therefor are outlined here:

- 1. The less the interval between generations is increased by progeny testing, the more likely it is that progeny testing will increase progress. This is illustrated by an example contrasting the results of selecting for weanling and yearling traits in sheep. Use of the best ram tested the year before on an optimum portion (60 to 70 percent) of the ewes increased progress by about 4 percent for weaning traits, but reduced it for yearling traits, as compared with progress to be expected from use of only the two best yearling rams each year. The only difference between these two examples is that 1 year is required to obtain progeny-test information on weanling traits, while 2 years are required for yearling traits.
- 2. When the rate of reproduction is low, progeny testing of sires is more likely to increase progress. The resulting increase in genetic superiority of parents tends to be larger, relative to the increase in age of parents, when there is less opportunity for early culling, particularly among females. For example, progeny testing affects progress more favorably for yearling traits in sheep than for growth rate in swine. Obviously, a much higher proportion of the female offspring must be retained in order to maintain the population in sheep than in swine.
- 3. If the basis for making early selections is relatively inaccurate, the progeny test is more likely to be effective. Therefore, the progeny test would be more apt to improve the annual progress in traits where

heritability is low, than in traits where it is high. Thus, the relative value of the progeny test is determined by a combination of circumstances that are largely beyond the breeder's control, and a regular plan of progeny testing is unlikely to increase (and may reduce) genetic progress unless the progeny-test information becomes available early in the animal's lifetime, the reproductive rate is low, and the basis for making early selections is relatively inaccurate. Dickerson and Hazel point out that improvement from selection is nearly maximum for most traits when culling is based on individual performance, family average, and pedigree, and when the interval between generations is kept short.

Dickerson and Hazel also studied the effectiveness of different methods of selecting for two specific characters in swine, growth rate of pigs and productivity of sows, and they have made some recommendations concerning the procedures that should be most effective. In selecting for growth rate, they recommend that 8 to 10 times as many boars and about 3 times as many gilts as are needed for breeding should be retained long enough after weaning (such as 180 days of age) to obtain a more reliable measure of growth rate than weaning weight. The rest may be culled without reducing appreciably the effectiveness of selection.

Several plans for culling were compared. Yearly progress from selection is greatest when sows are culled after the first litter, the best one-third to one-half being kept for a second litter 6 months later. Another plan, which is almost as effective, is to delay culling until after the second litter, and keep the best one-fifth to one-fourth of the sows for a third litter at 2 years of age. Progress is retarded by retaining more than the optimum proportion of older sows, because the less intense culling of sows and the longer interval between generations is only partly offset by the more severe culling of gilts and the greater accuracy of sow culling.

Having sows farrow two litters a year results in more rapid genetic improvement in productivity, since it permits the accuracy of selection of boars and gilts to be improved by basing the dam's productivity on two litters instead of one. It also permits the more productive sows to be kept for additional litters, with a minimum increase in the average interval between generations.

It is important that the breeder have effective yardsticks of merit, regardless of the selection procedures and breeding system he uses.

Evaluation of the fitted animal in the show ring has long been considered an important part of livestock improvement in the United States. In recent years it has become increasingly apparent that this procedure has many shortcomings as a tool in selection of improved breeding stock. For obvious reasons, only a small portion of the animals raised each generation can be prepared for evaluation. The condition of the animals at

the time of the show is usually highly artificial, and quite often is very different from the condition that is desired in practice. Undue attention is often given to so-called fine points of little or no economic importance. Some traits, such as milk yield and efficiency of feed utilization, cannot be accurately evaluated by visual inspection. The practice of excessive fitting has been carried over to the conditioning of breeding stock for sale, and is found to a marked degree even in bulls and rams that are to be sold for use on western ranges. Thus the breeder spends an undue amount for feed to put excessive fat on the animals, for which the buyer must pay, but for which he has no use. Also, the excessive fat may obscure defects in conformation, a point that is aptly stated in the common phrase, "Fat is a pretty color."

Recognizing the need for improved yardsticks, many workers have turned their attention to the development of measures of the economically important characters. Some characters, like litter size in swine, may be observed directly. Others, like body size, rate of growth, milk yield, yield of grease wool, and length of staple, can be weighed or measured directly. Others, for example face covering, skin folds, and body conformation in sheep, require indirect methods of evaluation and the assignment of a score to represent the degree of development in each animal. Devices have been developed for measuring such characters as length of wool fibers, tenderness of meat (muscle), and diameter of wool fibers, density of wool fibers, and hardness of fat.

Much attention also has been given to the measuring of functional traits, such as efficiency of feed utilization in beef cattle and swine, physiological response of horses and mules to exercise, and performance of work by draft horses and mules and by light horses in carriage and under saddle. Many of the developments are still in the experimental stage, but active research is continuing at many institutions to test existing procedures, to develop new ones, and to simplify experimental procedures so they may be applied by breeders in evaluating and selecting their stock.

Heritability

The development of an animal depends upon its inherited make-up and the environment in which it lives. Improvements in heredity are permanent, except those that result from particular combinations of genes, the determiners of heredity, and that disappear when the genes recombine. Improvements in environment must be provided again for each succeeding generation.

The heritability of a trait is actually a measure of the observed variation in a group of animals that is caused by differences in heredity. Estimates of heritability are based on the degree that related animals resemble each other more than less closely related or unrelated animals.

These estimates are applicable primarily to characters or traits in which development depends upon many genes.

Considerable information has accumulated in recent years on the heritability of various characters in livestock. The information helps the breeder because it indicates the progress that can be made by selection and the plan of breeding that is likely to be most effective. Practically all the information on heritability of economically important traits in livestock has been obtained during the last decade. A summary of it is given in the accompanying tables.

There are, of course, variations in the estimates of heritability, and many apparent discrepancies. There are several reasons. Errors may occur in sampling, particularly in studies based on small numbers of animals, so the results are not representative. Variations in environment

1. Estimates of heritability for weights of swine at various ages

Agc (days)	Herita- bility (percent)	Method used to determine heritability	Reference
Birth	4.6	Paternal half sibdododododododo	Lush et al. (1934). Baker et al. (1943). Nordskog et al. (1944). Krider et al. (1946). Nordskog et al. (1944).
21	$ \left\{ \begin{array}{c} 4 \\ 0 \\ 24 \\ 0 \end{array} \right. $	Paternal half sibdododododododo	Baker et al. (1943). Nordskog et al. (1944). Krider et al. (1946). Nordskog et al. (1944).
56	0 15 0 13.6	do	Comstock et al. (1942). Baker et al. (1943). Nordskog et al. (1944). Krider et al. (1946).
60	18	Intersire regressionCombination of different methods	Bywaters (1937). Do. Do.
84	$\begin{cases} 26 \\ 0 \end{cases}$	Paternal half sibdo	Baker et al. (1943). Nordskog et al. (1944).
112	28	dodo	Baker et al. (1943). Nordskog et al. (1944).
140	19 21	dodododo	Baker et al. (1943). Nordskog et al. (1944).
150	16 13. 7	Line difference due to selection Paternal half sib	Krider et al. (1946).
168	25 27	dodo	Baker et al. (1943). Nordskog et al. (1944).
180	14 20 62 30 40 30 23 19 23. 9	Intrasire regression Paternal half sib Intrasire regression Intrasire regression Intrasire offspring-dam correlation Full sibs, not litter mates Regression of variance to genetic relationship. Paternal half-sib and intrasire regression. Line differences due to selection Paternal half sib	Comstock et al. (1942). Whatley (1942). Do. Do. Do. Do. Whatley and Nelson (1942).

2	Ferimates	of heritability	for pain and rate	of gain in swine
Z.	Estimates	of neritability	ior gain and rate	or gain in swinc

Period (days) Heritability (percent)		Méthod used to determine herita- bility	Reference	
Birth-21 Birth-56	7 15	Paternal half sib	Baker et al. (1943). Hazel et al. (1943). Nordskog et al. (1944).	
21–56		dodo Intrasire regression Paternal half sib	Baker et al. (1943). Nordskog et al. (1943). Nordskog et al. (1944).	
56–84	6 25.8	do Intrasire regression Paternal half sib	Baker et al. (1943). Nordskog et al. (1944). Do.	
84–112	31 10 27.8	do	Baker et al. (1943). Nordskog et al. (1944). Do.	
112–140	4 10 24, 5	Intrasire regression	Nordskog et al. (1944). Do.	
140–168	10	do	Baker et al. (1943). Nordskog et al. (1944). Do.	
56–112	[28	do	Hazel et al. (1943).	
56–168	45. 3 17	do	Nordskog et al. (1944). Hazel et al. (1943).	
50-200	26	Intrasire regression	Comstock et al. (1942).	
56-200	\{ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \	Paternal half sib	Nordskog et al. (1944). Comstock et al. (1942).	
Birth-200	{ 21 3	Paternal half sib	Nordskog et al. (1944). Do.	
Weaning-200.	21 24	Average of three methods	Do. Lush (1936).	

may be correlated for certain kinds of relatives. For example, data may have been collected over a period of years in which gradual changes in feed or management occurred. Thus, both dams and their progeny, raised at various times during this period, may have been exposed to an environment better or poorer than the average. Such environmental contributions to likenesses between relatives are difficult to measure. Another factor that may affect estimates of heritability is the mating system. A different approach is required to obtain a reasonably accurate estimate of heritability in an inbred population than in one where random mating has been practiced, a factor that has not been taken into account in some of the studies. In others, the mating system or the amount of inbreeding may have deviated more (or less) from random than the investigator supposed.

Data on the heritability of weights of swine at various ages, and on the heritability of rate of gain (tables 1 and 2) indicate that the estimates of heritability increase as pigs grow older. Therefore, selection for maximum weight should be most effective if practiced at 180 days, rather than at earlier ages. Heritability of weight at 180 days approximates 30 percent. This means the breeder should expect to make about 30 percent of the

progress he "reaches for" in selection. For example, if he selects for parents of the next generation animals that weigh 20 pounds above the average of his stock at 180 days, their offspring should be expected to weigh about 6 pounds more than the average of offspring from parents picked at random from the same stock.

3. Estimates of heritability for fertility in swine

Measure of fertility	Herita- bility (percent)	Method used to determine heritability	Reference
Litter size at birth.	17 10 17 18 34 44 13 15. 6 14. 8 13. 6 14. 5	Maternal half-sib litters Estimated from published reports of various workers. Maternal half-sib litters Paternal half sib Full sib Intrasire regression Average of three methods	Do. Hetzer et al. (1940). Stewart (1945). Do. Do. Do. Do.
Live pigs far- rowed. Litter size at 28 days. Litter size at 70 days. Litter size at weaning.	17. 6 8. 8 15. 8 13. 6 16 20 17	Paternal half sib. Full sib. Intrasire regression. Average of 3 methods. Maternal half-sib littersdo	Do.

4. Estimates of heritability for other characters in swine

Character	Herita- bility (percent)	Method used to de- termine heritability	Reference
Weaning weight of litter.	18	Maternal half-sib lit- ters.	Lush and Molln (1942).
Productivity index of sow	16	Intrasire regression	Hazel, quoted by Lush and Molln (1942).
Economy of gain	18	Average of 3 methods.	
Body length		do	
Yield of export bacon	20	do	Do.
Thickness of belly	46	do	
Thickness of back fat		do	
Market score at slaughter			Whatley and Nelson (1942).
Conformation score	20	Intrasire regression	
Type score (within , strains).	38	Paternal half sib	Hetzer et al. (1944).
Type score (between strains).	92	do	Do.

¹ Minimum estimate.

5. Estimates of heritability for various characters in beef cattle

Character	Herita- bility (percent)	Method used to determine heritability	Reference
	23	Paternal half sib	Knapp and Nordskog (1946).
	42	Sire-offspring regression	Do.
	34	Sire-offspring regression	Do.
Birth weight	!}	within year.	
Ü	29	Paternal half sib	Dawson, Phillips and Black (1947).
	11	Paternal half sib;	, ,
	: \	corrected birth weights.	Do.
	12	Paternal half sib	Knapp and Nordskog (1946)
Weaning weight	₹ 0	Sire-offspring regression	Do.
	30	Sire-offspring regression within year.	Do.
	(81	Paternal half sib	Do.
Final food lot weight	[] 69	Sire-offspring regression	Do.
Final feed-lot weight	94	Sirc-offspring regression within year.	Do.
	99	Paternal half sib	Do.
Gain while on feed	[] 46	Sire-offspring regression	Do.
Gain while on leed	97	Sire-offspring regression within year.	Do.
	75	Paternal half sib	Do.
Earnamer of main	54	Sire-offspring regression	Do.
Economy of gain	18	Sire-offspring regression within year.	Do.
	53	Paternal half sib	Knapp and Nordskog
Score at weaning	K		(1946a).
S	l 0	Sire-offspring regression	Do.
Slaughter grade	63	Paternal half sib	Do.
Carcass grade	84	do	Do.
Dressing percent	1	do	Do.
Area of eye muscle	69	do	Do.
*	!		

Litter size at birth is not so highly inherited as weight at 180 days. The unweighted average of the eleven estimates given (in table 3) is 19.2 percent. This means that the breeder can expect to realize about one-fifth of the progress in litter size that he reaches for in selecting the parents of the next generation. If selection for litter size is based only on sows, no attention being given to boars in this respect, then the progress will be only about one-half of one-fifth. The estimates of progress through selection are based on the assumption that all the heritability for each trait is due to additive effects of genes. If a portion of it is due to epistatic effects (interactions between different pairs of genes), the effectiveness of selection would be somewhat less.

Estimates of heritability for a number of other characters in swine have also been obtained (table 4), but only one study has been made of each of these characters, except type scores, for which there are two figures. The estimate for type score (between strains) is exceptionally high, 92 per-

cent. This was obtained on a combination of three populations representing large, medium, and small-type Poland China swine, and indicates that the differences between these three strains were largely due to heredity. The estimate of 38 percent for type score (within strains) is the one that indicates the approximate amount of progress that might be made in selecting for type within one of the strains or in a relatively uniform breed. Most of the estimates of heritability for other traits are sufficiently high to indicate that fairly rapid progress can be made by selection. The estimate for economy of gain is quite low, and, if representative, indicates that little improvement could be made per generation as a result of selection for this trait. Further studies are necessary to establish, within reasonably accurate limits, the extent to which these and other important traits of swine are inherited.

We have estimates of heritability for a number of characters in beef cattle (table 5). Some of these are higher than seems reasonable in comparison with the figures obtained from swine and sheep and in view of the probable effects of environmental factors on such characters as final feedlot weight, rate of gain, and economy of gain in the feed lot. More information is needed before these figures can be accepted as generally representative, but at least they indicate that selection should be effective in improving most of the characteristics studied.

Data on heritability of various characters in sheep (table 6) also indicate that most of the various desirable traits studied can be improved by selection, although selection for such traits as yearling body score, type score at weaning, and condition score at weaning would not lead to rapid progress. The several figures for heritability of skin folds and those for face covering indicate that it should be possible to make rather rapid progress in the elimination of excessive skin folds and covered faces by selection for animals that are smooth and have open faces. One of the figures for heritability of neck folds (8 percent) is low, but it was obtained on breeds that are characterized by relatively few skin folds compared with the Rambouillet, on which the other estimates for this character are based.

The heritability of a trait is one of the most important factors to consider in deciding upon the breeding plan that is most apt to be successful in bringing about improvement in that trait. If the heritability of the desired trait is high, the best method of breeding to bring about improvemen will be the mating of animals possessing greatest development of the desired trait, little use being made of information on pedigrees and relatives. If heritability is low, the breeder is more apt to make progress if he uses information on pedigrees and collateral relatives and information he gets from progeny tests in deciding which animals to use for breeding. Also, if heritability is low, it is generally advisable to make relatively little use of inbreeding other than the inbreeding that is needed to make

6. Estimates of heritability for various characters in sheep

Character	Herita- bility (per- cent)	Method used to deter- mine heritability	Reference
Birth weight	30	Paternal half sib	Chapman and Lush (1932).
Yearling staple length	36	Intrasire regression	Terrill and Hazel (1943).
Yearling weight of clean wool.	38 28	do	Do. Do.
Yearling body weight	40 12	do	Do. Do.
Yearling body score Face covering	32	do	Do.
Neck folds Body folds	26 37	do	Do. Do.
Weaning weight	26. 9	Paternal half sib	Hazel and Terrill (1945).
	17.0	Average 3 breeds, 2 methods	Hazel and Terrill (1946a).
	33. 9	Intrasire regression	Hazel and Terrill (1945).
Staple length at weaning.	30	Weighted average of 2 methods.	Do.
Stapic length at wearing.	41	Paternal half sib	Do.
	38. 7 40	Intrasire regression Weighted average of 2	Do. Do.
	43.0	methods. Average 3 breeds, 2	Hazel and Terrill
	15.2	methodsPaternal half sib	(1946a). Hazel and Terrill
	6.8	Intrasire regression	· (1946). Do.
Type score at weaning	13.0	Weighted average of 2 methods.	Do
	7.0	Average 3 breeds, 2 methods	Hazel and Terrill (1946a).
	2.4	Paternal half sib	Hàzel ánd Terrill (1946).
Condition score at wean-	13.8	Intrasire regression Weighted average of 2	Do. Do.
ing.	21.0	methods. Average 3 breeds, 2	Hazel and Terrill
	45.6	methods	(1946a). Jones et al. (1946).
Skin folds	51.2	Average of 4 methods, within year.	Do.
	36. 2	Paternal half sib	Terrill and Hazel (1946).
Neck folds	45. 1 39	Intrasire regression Weighted average of 2	Do. Do.
	8	methods. Average 3 breeds, 2	Hazel and Terrill
	51.0	methods Paternal half sib	(1946a). Terrill and Hazel
Face covering	60. 3	Intrasire regression Weighted average of 2	(1946). Do. Do.
	46.0	methods. Average 3 breeds, 2	Hazel and Terrill
Normalian - Control 1	! (_ methods	(1946a).
Number of nipples Number of functional	14. 4 5 26	Intrasire correlation	Phillips, et al. (1945). Do.
nipples.	22	Intrasire regression	Do.

families distinct from each other or to make full use of the progeny test.

Heritability of a trait may be due to additive effects of genes, or there may be variations in hereditary effects owing to epistatic effects of genes, or both types of effects may be present. The difference between these two types of effects may be illustrated by supposing that two dominant genes, A and B, located at different points on a chromosome or on different chromosomes, have values of 6 and 4, respectively, when one occurs without the other, insofar as they affect a certain trait. If their effects are strictly additive, the combined value of the two is 10, if both are present in an animal. If, however, the value is 12 when they occur together, the effects are not strictly additive, and the extra value resulting from the interaction of the two is called an epistatic effect. If additive effects of genes are low, but heritability of a trait appears to be fairly high because of epistatic effects, inbreeding to develop lines that are distinct from each other, selection of the outstanding lines, crossing these lines, and developing new ones from the more favorable crosses is the procedure that appears most likely to be effective.

There is need for much additional information on heritability of various economically important traits in livestock, and on the nature of the effects of genes that control the development of these traits, before it will be possible to prescribe methods of breeding that will be most effective in all situations with which breeders are confronted. However, sufficient information is available to indicate some of the advantages and limitations of inbreeding and crossing, and the possibilities of developing new types from crossbred foundations. These problems are discussed later.

Inbreeding

Inbreeding is the mating of animals that are more closely related to each other than the average relationship within the population concerned. Such matings tend to make the offspring more homozygous, on the average, than if their parents were of average relationship to each other. Genes occur in pairs. If both members of a pair are alike they are said to be homozygous; if they are different they are said to be heterozygous. Thus, inbreeding increases the proportion of pairs of homozygous genes, or determiners of heredity.

The results achieved by corn breeders with inbreeding and crossing of inbred lines seemed to justify investigations into the possibilities of speeding up livestock improvement by establishing inbred lines and testing the usefulness of these lines in various types of crosses. Hence, much work has been initiated in recent years. The major projects in this field are being conducted cooperatively by the Bureau of Animal Industry of the Department of Agriculture and various State experiment stations through the Regional Swine Breeding Laboratory, whose head-

quarters is in Ames, Iowa; the Western Sheep Breeding Laboratory at Dubois, Idaho, and the United States Range Livestock Experiment Station at Miles City, Mont. Work at Miles City is primarily with range beef cattle, but a limited amount of work is also under way with swine. Extensive work with swine, sheep, and cattle is also in progress at Beltsville.

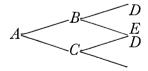
Since inbreeding is the most powerful tool the breeder has for establishing uniform strains or families that are distinct from each other, and since much experimental work is now being conducted to determine how best to use it in livestock improvement, many readers may wish to know how the amount of inbreeding is measured.

The method that is now used almost exclusively was developed by Sewall Wright, formerly of the Department. His formula is:

$$F_x = \Sigma(\frac{1}{2})^{n+n'+1}(1+F_n)$$

The formula appears more technical than it actually is. F_x stands for the coefficient of inbreeding of an animal, which is to be calculated. The Greek letter Σ (sigma) represents all the hereditary contributions to the inbreeding, but has no numeral value of its own. For example, if two or more ancestors contribute to the inbreeding, the contribution of each is calculated and then all are added together to obtain the coefficient of inbreeding. The fraction $\frac{1}{2}$ is the animal's relationship to each of its two parents; n stands for the number of generations between the sire and a common ancestor; n' stands for the number of generations between the dam and a common ancestor. The factor $(1+F_a)$ represents the influence of a common ancestor, if that ancestor is itself inbred. If the common ancestor is not inbred, this part of the formula is omitted.

To illustrate, suppose an animal, A, has the following ancestors:



The animal has the same grandsire, (D), on both the sire's (B) and dam's (C) sides of the pedigree. Thus D is a common ancestor of both parents of A. Since there is only one generation between B and D, and also one between C and D, the value for C and C in the formula are 1 and 1, thus:

$$F_x = (\frac{1}{2})^{1+1+1} \text{ or } (\frac{1}{2})^3$$

The third power or the cube of $\frac{1}{2}$ is $\frac{1}{8}$, which is expressed as 12.5 percent, and is the coefficient of inbreeding.

This coefficient indicates the increase in the proportion of homozygous pairs of genes that can be expected, on the average, in matings where

there is one common grandparent, as compared with matings where there is no common ancestor. If we suppose that random breeding had been practiced in a herd, and that 50 percent of the pairs of genes were homozygous and 50 percent heterozygous, then 12.5 percent inbreeding would imply that 12.5 percent of the heterozygous pairs were homozygous in the new individual (12.5 percent of 50 is 6.25)—so, 56.25 percent of the pairs would be homozygous, while 43.75 would be heterozygous.

If the common ancestor, D, in the above example had already been inbred, for example 25 percent, then the factor $(1+F_a)$ would have been (1+0.25) or 1.25, and the inbreeding of animal A would have been 12.5×1.25 or 15.625, usually shortened to 15.6 percent.

Inbreeding does not create nor destroy any genes—it merely permits more of them to occur in homozygous pairs. Genes that favor development of both desirable and undesirable characters may become homozygous. Inbreeding thus uncovers many recessive genes that would otherwise remain concealed by their dominant-pair mates, or allcles (a recessive gene is one that is not able to express itself when it occurs as the pair-mate of a dominant gene, hence only the effect of the dominant gene is seen). Recessive genes generally have less desirable effects than dominant genes, so there is usually some degeneration in the average merit of individual animals when inbreeding is practiced. The chief danger of intense inbreeding, therefore, is that it may make undesirable genes homozygous so rapidly that it will be impossible to discard all the individuals that are homozygous for them.

The chief advantages of inbreeding are: It helps to uncover undesirable recessive genes so that animals possessing them may be culled; it may be used to develop uniform and distinct families so that interfamily selection may be more effectively practiced; new and often superior groups of animals may be produced by combining two or more inbred lines; it increases prepotency by increasing the chances that animals will pass on their traits to their offspring; and it is useful in maintaining a high relationship of stock to an especially desirable ancestor.

The extent of the experimental work that is being undertaken to test the possibilities of using inbreeding in livestock improvement can best be shown by details from some places where the work is being done.

The Regional Swine Breeding Laboratory and the cooperating State agricultural experiment stations in Illinois, Indiana, Iowa, Minnesota, Missouri, Nebraska, Oklahoma, and Wisconsin have a total of 46 lines of swinc. These include 19 Poland China, 11 Duroc-Jersey, 4 Hampshire, 8 Chester White, and 1 Landrace line, and 3 lines that are being developed from crossbred foundations.

Eight new lines are being developed by the Bureau of Animal Industry at Beltsville. Another line is being developed in cooperation with the Maryland Agricultural Experiment Station, and two additional lines

are being developed at Miles City, in cooperation with the Montana Agricultural Experiment Station.

Thirty-two lines of Rambouillet sheep are being developed at the Western Sheep Breeding Laboratory, Dubois, Idaho. In addition, the Bureau of Animal Industry is developing 10 lines of Columbia and 10 of Targhee sheep at the United States Sheep Experiment Station, which also is located at Dubois.

A few lines of beef cattle are being developed by the Bureau of Animal Industry and the Montana Agricultural Experiment Station at the United States Range Livestock Experiment Station at Miles City. Plans have been developed to establish up to 30 or 35 lines in cooperation with several State experiment stations in the range-cattle area, and lines of beef and dual purpose cattle are being established at Beltsville.

Breeding work with livestock progresses slowly, for obvious reasons. The reproductive level is low, compared with plants, and the time required for a generation is long. The long time per generation is illustrated by the following estimates made by Jay L. Lush: Horses, 10 to 13 years; beef cattle, 4.5 to 5 years; dairy cattle, 4 to 4.5 years; sheep, 4 to 4.5 years; swine, about 2.5 years. Also, with the exception of swine, a large proportion of the female progeny reared must be retained as replacements in order to maintain numbers. Lush gives the following estimates of the percentages of females that must be retained for this purpose: Horses, 35 to 45; beef cattle, 40 to 55; dairy cattle, 50 to 65; sheep, 45 to 55; swine, 10 to 15. While these factors, over which the breeder has no control, place limits on the rate of progress, they also make it imperative that the most effective methods of selection and breeding be used if the breeder is to have much real genetic progress to show for each generation of breeding effort. And despite the handicaps that limit the rate of progress in animal-breeding experimentation, much has been learned in recent years from the work with inbreeding of livestock.

That work has not progressed to a point where broad generalizations can be made, and many details of application of results must yet be worked out, but the results to date indicate that the breeder can make effective use of this tool in speeding up improvement. The work with swine naturally has gone ahead more rapidly than the work with sheep and beef cattle. To illustrate what is being accomplished, I outline some of the results in the Regional Swine Breeding Laboratory, which was established in 1937, with W. A. Craft as director, and the eight State experiment stations that are conducting projects in this regional effort, under the leadership of J. L. Krider (Illinois), J. R. Wiley (Indiana), Jay L. Lush (Iowa), L. M. Winters (Minnesota), L. A. Weaver (Missouri), M. L. Baker (Nebraska), O. S. Willham (Oklahoma), and A. B. Chapman (Wisconsin).

Increased inbreeding has generally been accompanied by some deterioration in the productivity of swinc. This was expected, in view of the results obtained earlier with laboratory animals and corn. It has generally been more difficult to maintain vitality and litter size than growth rate in lines of swine that were being inbred.

Crossing of inbred lines has usually corrected the decline in performance that accompanied inbreeding, and in some cases appears to result in a considerable increase over the performance of noninbred stock.

Inbred lines developed from widely unrelated stock have produced more favorable results when crossed than lines developed from related stock. Inbred lines from different breeds have given more favorable results in crosses than those from the same breed.

The mating of inbred boars of selected inbred lines to noninbred sows appears to give a little increase in the performance of the pigs, in comparison with pigs from similar sows and sired by noninbred boars.

Inbreeding of 30 to 40 percent appears to be enough to make it possible to determine the value of a line of swine, and to make lines differ genetically, particularly if the lines are from unrelated stock. This is equivalent roughly to about 2 generations of brother-sister mating, 4 generations of half-brother-sister matings, or 12 generations of breeding in which single first cousins are mated.

Lines that were inbred 30 to 40 percent have been found to differ in physiological characters that were not evident in the appearance of the animals. For example, boars in different lines at the Minnesota station have been found to differ in the amount of male hormone excreted in the urine and in the rate of development of the testes.

Selection for one character may in some cases give rise to a change not desired by the breeder in another character. There is some evidence, for example, that maximum rate of fattening seems to be opposed to litter size and milking ability in sows. Some of the breeder's effort is canceled by the compromise necessary in selection between various characters. Studies now in progress have revealed that hereditary factors of the individual pig that cause rapid and economical gains when the pig is full-fed to 225 pounds, and that also lead finally to high ratings for conformation in the live pig, are largely the same features that cause rapid deposition of fat, resulting in fat carcasses at the time of slaughtering. These results tend to emphasize that selection based on conformation at market weight according to present standards constitute selection for fatter hogs because the differences in width, depth, and plumpness of body, which loom large in making choices, are largely differences in amount of fat.

Thus, it is evident that some compromise must be made in selections, and that care must be exercised to avoid selecting in an undesired direction. Sows possessing and transmitting the ability to fatten rapidly tend

to be poor in suckling ability, and thereby reduce the gains and increase the feed requirements of their pigs during the period of fattening. It appears now, therefore, that in selection for rapid and economical gains, the indirect selection for fat carcasses associated with the most rapid gains may be offset if selections are based on individual gains of pigs during the early part of the growth period, perhaps at 85 to about 112 days of age, when more of the weight is muscle than later, and by giving much attention to suckling ability of sows, which is indicated by litter size and weight of pigs at 3 to 8 weeks of age.

Not all lines developed in any program with swine, or with other classes of livestock, will be valuable for use in livestock improvement. For example, it is becoming apparent that only a part of the 46 inbred lines of swine on hand in the Regional Swine Breeding Laboratory program will merit maintenance and use for improving purebred herds and for extensive use in pork production. Some wastage of lines is inevitable. Many inferior lines of corn have been discarded, and the same will apply to inbred lines of livestock. E. W. Lindstrom of Iowa made a survey of the results of inbreeding of corn (maize) in 1939, and estimated that only 2.4 percent of a total of about 30,000 inbred lines developed in the United States during several previous years had proved useful.

The expense of developing an inbred line of livestock is of course much greater than for a line of corn. For this reason, it is generally desirable to guide the development of lines as much as possible by selection, and to test them thoroughly before deciding to retain or discard them. But for the same reason, it is necessary to be ruthless in discarding lines, once it is clearly demonstrated that they can make no worthwhile contribution to improvement, rather than to follow a natural desire to retain expensive (but not valuable) stock with the hope that it may prove useful.

The outstanding inbred lines of swine may be used for crossing with noninbred stock or for crossing with other inbred lines to produce market hogs, or they may be used for crossing with other lines to develop still better lines from which stock will be available for use in commercial production or for improving purebred herds. The situation will be somewhat different for cattle and sheep than for swine. Since such a large proportion of the female offspring in inbred lines of cattle and sheep must be retained for replacements, the numbers that can be used for crossing with males from other lines for commercial production will be small. Experimental work has started to test the various ways of utilizing inbred lines, and further results should be had before recommendations are made.

One of the most urgent problems in connection with the use of inbred lines is the development of methods of preserving them and guarding their purity. The experiment stations cannot continue to maintain established lines indefinitely. Just as they developed many inbred lines of corn and placed them in the hands of organizations that were producing hybrid seed commercially, the inbred lines of livestock which they develop must be placed in the hands of private breeders who will expand numbers and make stock available to commercial livestock producers. Limited attempts are already being made to place some inbred swine in the hands of private breeders. Ways to guard the purity of the lines are yet to be found.

It is possible that the existing breed associations and their purebred-breeder members will take over this work as an additional function of the purebred association for each breed involved. This would be a logical development, and in the initial stages might be carried out with the help and guidance of the experiment stations that are developing the lines. If the associations do not expand their services to meet this need as it arises, other methods must be found. It is difficult to predict how rapidly the need will expand, but it should be remembered that the extensive hybrid-seed corn industry of today had its beginning only in 1926, when the first seed company was organized for the commercial production of hybrid corn, and that the first appreciable expansion began about 1932, when hybrid-seed production was taken up by several new companies.

Cross-breeding

Cross-breeding for the production of market animals has been practiced for many years, particularly with swine, sheep, and beef cattle. By this method of breeding, producers have taken advantage of the increased productivity (called hybrid vigor or heterosis) that frequently results from the crossing of distinct types and breeds.

The most extensive experimental work in this field has been with swine. J. L. Lush, P. S. Shearer, and C. C. Culbertson of Iowa State College have summarized the results of the important experiments in this field. They point out that any one piece of work, especially one in which small numbers of pigs were used, scarcely appears enough by itself to prove beyond question that there is a real advantage in favor of cross-breeding. Yet, almost every piece of work indicates that such an advantage is probable.

The Iowa workers conclude that the combined weight of all the scattered evidence is overwhelming in indicating that cross-breeding results in increased production. Crossbred pigs tend to be somewhat more vigorous and thrifty than would be expected from the average of the two parent breeds. Because of this added vigor, crossbreds generally show a lower death rate up to weaning, and consequently larger and heavier litters are weaned. Also, they generally gain a little more rapidly on a little less feed than the purebreds. For the same reasons, the cross-

bred gilts or sows, when used for breeding, can be expected to wean slightly larger and heavier litters than purebreds. Lush and his coworkers emphasize that these are results that can be expected on the average, but they should not be expected to happen every time a cross is made, any more than slightly loaded dice should be expected to turn up a winning combination every time they are thrown.

Three general systems of cross-breeding may be practiced by the producer of market hogs. Purebred or high-grade females of one breed and purebred boars of another breed may be used for the production of each crop of pigs. This plan is simple, but it means that replacements of sows must be purchased or produced in a subsidiary breeding program.

Another plan is called crisscrossing, in which boars of two breeds are alternated in producing each new generation of pigs from dams saved from the previous generation. This plan takes advantage of any hybrid vigor expressed in the ability of the crossbred dam to raise large, vigorous litters, and eliminates the necessity of purchasing sow replacements.

Still another plan utilizes three breeds of boars. It is similar in all other respects to the crisscrossing system.

Our knowledge of the results that may be expected from crossbreeding beef cattle has been increased in recent years through work conducted cooperatively at Miles City, Mont., by the Department and the Montana Agricultural Experiment Station. The experiment was planned to test the possibility of maintaining heterosis through three-breed crossing. The first cross was Shorthorn bulls on Hereford cows. The first generation, or F_1 , females (offspring of Shorthorn bulls and Hereford cows) were mated to Aberdeen-Angus bulls, and their triple-cross female offspring were mated to Hereford bulls. The latter phases of this work have not yet been completed, but results thus far indicate that three-breed crossing may be an effective method of increasing productivity in beef cattle. Some results:

Fifty-seven F₁ steers (Shorthorn × Hereford) were compared with 67 Hereford steers. The crossbred calves gained more rapidly in the feed lot and were heavier at the time of marketing. Crossbreds had fewer digestive disturbances, and they also had higher dressing percentages. Differences in efficiency of feed utilization, slaughter grade and carcass grade were not significant.

Fifty-three F₁ and 55 Hereford heifers were also compared. The crossbred heifers were heavier at birth and weighed 7.2 pounds more at weaning time. At 18 and 30 months the differences in favor of the crossbreds were 50.9 and 88.0 pounds, respectively.

Results with offspring produced by mating Λ berdeen-Angus bulls to F_1 females show that the triple-cross steers weighed more at weaning and at the end of the feeding period, gained more rapidly during the feeding period, sold for more per pound and per head, had a higher dressing percentage, and returned more per head above feed and

marketing costs than the Hereford steers with which they were compared. The triple-cross heifers also weighed more at weaning and at 18 months, and were given higher scores at 18 months than Hereford heifers raised under identical conditions. There were indications that the triple-cross calves had a faster rate of gain before weaning, but a slower rate after weaning than F_1 calves.

Further work is needed to determine the part that continued three-breed crossing can play in commercial beef production. Management of animals in several groups at breeding time may make it difficult for some producers to follow. Crisscrossing, in which only two breeds are used, should be more practical, and its use should be tested further experimentally.

Developing New Breeds

Many breeds of livestock have been developed. They vary widely in traits and adaptability. But circumstances sometimes arise in which no one of the existing breeds meets all the requirements of the breeder. Under such circumstances, it may be desirable to develop a new breed, combining characteristics of two or more breeds. An example of this is the Columbia sheep, which has become sufficiently well established to be recognized as a breed.

It has been rather common range practice for several decades, in some western areas, to cross-breed sheep by mating range ewes that predominate in Rambouillet or other fine-wool breeding with rams of long-wool breeds, such as Lincolns and Cotswolds, in order to get larger ewes that produce more lambs and pounds of marketable wool than can be produced with fine-wool ewes of the parent stock. Although the practice has advantages, it has given rise to considerable periodic variation in flocks because crossbred ewes that were produced in this way were, as a rule, alternately mated to fine-wool rams and then to long-wool rams.

In an effort to contribute stability to the production of large range ewes, the Columbia sheep has been developed by the Department. This breed is, in general, the result of cross-breeding select Lincoln rams with Rambouillet ewes and proceeding from this original crossbreed foundation by mating the most select first-cross rams with carefully selected first-cross ewes and interbreeding the rams and ewes descending from them. This undertaking was pursued at Laramie, Wyo., from 1912 to 1917, and since that time this development of the Columbia sheep by the Department has been conducted at the United States Sheep Experiment Station at Dubois, Idaho.

The Columbia is a white-faced sheep that is large, vigorous, moderately low-set, polled, and free from wool blindness and body wrinkles. The good body length balances well with the width and depth. It is

especially well-fleshed in the loin, and has a square rump and a good leg of mutton. Mature rams range in body weight from 190 to 250 pounds, whereas mature ewes range from 135 to 155 pounds under range conditions in the fall. On the average, mature Columbia ewes produce about 12 pounds of unscoured wool per year, which, on a commercial basis, yields approximately 50 percent scoured clean wool. The average length of staple of the fleeces of 1 year's growth is approximately $3\frac{1}{2}$ inches. Mature rams produce fleeces weighing 18 pounds or more for a growth of 12 months under range conditions. The annual length of staple for fleeces of rams averages about $3\frac{3}{4}$ inches. The fleece tends to stay well together in storms. Desirable market grades of the wool from Columbia sheep, on the basis of fineness, as determined commercially, are Three-eighths Blood and Quarter Blood.

Work of this type is also under way at other places, and with other types of livestock. The Department, working in cooperation with the Office of Indian Affairs, is developing a type of sheep that is adapted to the semiarid ranges of the Southwest and produces a good-quality carpet wool suitable for hand weaving. This work is conducted at the Southwestern Range and Sheep Breeding Laboratory, Fort Wingate, N. Mex. At its Iberia Livestock Experiment Farm, near Jeanerette, La., the Department is establishing and testing new lines of cattle containing varying amounts of zebu and Aberdeen-Angus blood.

The object of this work is to develop a type or types of beef cattle that can perform satisfactorily in the subtropical conditions along the Gulf of Mexico. Work is also under way with swine, in efforts to develop improved types having more lean and less fat, by combining the Danish Landrace (a bacon type) with various domestic and imported breeds of the fatter, or lard, type. The Bureau of Animal Industry has a number of these experimental lines at Beltsville and one at its Range Livestock Experiment Station in Miles City, Mont. The Minnesota Agricultural Experiment Station is also developing some new lines of swine. There are other experimental efforts of this type, but these should serve to illustrate the nature of the work being done.

The development of a new breed is not a task to be undertaken lightly. A definite need for a new type should be clearly evident before such a project is undertaken. Facilities should be available to handle a large number of animals and to continue the project for many years, so that the new type may be well established. The person or persons planning and supervising the work should have a clear understanding of the genetic principles involved. Work like this is obviously limited to Federal and State experiment stations and to the establishments of a limited number of private breeders who have unusual facilities and are willing to venture from the established breeding practices.

Maintenance of a satisfactory level of reproduction is essential to the

success of any breeding program. Much work has been done in recent years on various phases of physiology of reproduction that have a bearing on fertility.

The importance of time of breeding in relation to the beginning and end of the heat period, or estrus, has received considerable attention. Data on length of estrus, time of ovulation, or release of the egg or eggs from the ovaries, speed of travel of spermatozoa in the reproductive tract, duration of life of spermatozoa in the female tract, and studies on the proportions of successful matings when breeding takes place at various stages of estrus all bear on the problem.

Some Factors Affecting Reproduction

The combined evidence from many sources indicates that a mating has the greatest chance of being successful if it takes place near the time of ovulation. In the various types of farm animals, recommended times of mating where hand mating is practiced are:

Horses—If mated only once, the third day of estrus appears best, on the average. If service can be had more than once, the best practice appears to be to mate on the third day, and on every second day thereafter until the end of estrus.

Cattle—If bred once, mate 12 to 20 hours after onset of estrus. If bred twice, mate immediately after onset of estrus and again 12 to 20 hours later.

Sheep—During the second half of estrus. If feasible, mate about 12 hours after estrus begins and at 12-hour intervals until estrus ends. Estrus lasts about 30 hours, on the average.

Goats—During the second half of estrus. Exact data are not available, but the duration of estrus is similar to that in the ewe.

Swine—Late on first day, or preferably on second day of estrus.

We conducted studies at the Utah Agricultural Experiment Station to determine if giving special feed to range lambs would influence sexual development and reproduction. The first winter is perhaps the most critical time in the development of the range cwe. Up to weaning, the lamb is provided with a reasonably adequate diet in most cases, while with its dam on spring and summer range. When the lamb is weaned and moved to winter range, there is often a decided drop in level and quality of nutrition, and this is accompanied by more severe environmental conditions in other respects.

Results of the study in Utah indicate that when ewe lambs are given special feed during the first winter the reproductive tract develops more fully, as compared with development in ewe lambs maintained on open range. These results, coupled with results of earlier work by A. C. Esplin, M. A. Madsen, and the writer in which larger lamb crops were produced

at 2 years of age as a result of lot feeding during the first winter, indicate the desirability of giving special attention to the feeding of ewe lambs in range flocks. How far the rancher can afford to go in giving special attention to his ewe lambs is a problem needing further investigation.

The environment in which animals live may affect the fertility of live-stock. An experiment has been conducted cooperatively by the Bureau of Animal Industry and the Florida Agricultural Experiment Station which gives some clear experimental evidence on this point. Thirty pairs of Columbia ewes and two pairs of rams were selected from the Department's flocks at the Dubois station. One member of each pair was retained at Dubois, and the other sent to the North Florida Experiment Station at Quincy. Wool production of the ewes at Quincy was comparable in grease weight and staple length to that of the ewes at Dubois, but the level of fertility as measured by percent of ewes lambing was not as high. This deficiency was especially marked during the first two years the ewes were at Quincy. Columbia ewes descended from those brought from Dubois and raised at Quincy also reproduced at a lower level and had smaller lambs at weaning than Columbia ewes at Dubois, but there was no noticeable reduction in wool production.

Most sheep and goats breed naturally during the fall and early winter months. In some instances, there would be an economic advantage in having part or all of the ewes and does in a flock bred during the spring or summer months. The possibility of stimulating estrus and ovulation in ewes and does during the spring and summer has received much attention in recent years. It has been possible to induce ovulation in a high proportion of the animals by the use of gonadotropic hormones, but induction of estrus in conjunction with ovulation has been quite erratic. No satisfactory explanation of these variable results has been found.

Fertility, as measured by percentage of conceptions, is generally lower in animals in which estrus has been induced or in those force-mated after induction of ovulation, than in animals bred during natural estrus. However, satisfactory fertility has been reported in some cases. Further work is needed to determine the endocrine physiology of normal and experimentally induced estrus in sheep and goats and the specific doses and time sequences that will induce estrus and ovulation, before procedures can be recommended for general use in practice.

THE AUTHOR

Ralph W. Phillips was formerly in charge of genetics investigations in the Bureau of Animal Industry. He took leave during 1943 and early 1944 to help the Governments of China and India with their livestock problems. Dr. Phillips is editor of the Journal of Animal Science and is the author or coauthor of about 100 publications on various phases of animal breeding. He is a graduate of Berea College and took graduate work at the University of Missouri.

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